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PHYSIOLOGICAL RESPONSES OF OLD GROWTH PONDEROSA PINE AND WESTERN LARCH TO RESTORATION CUTTING AND BURNING TREATMENTS

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Physiological responses of old growth ponderosa pine and western larch to restoration cutting and burning treatments

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Abstract

In the interior northwest, harvesting of old growth trees and fire exclusion since the early 1900's has resulted in a successional replacement of open ponderosa pine and western larch stands to stands of interior Douglas-fir. The strong competition with the Douglas-fir understory decreases resource availability for old growth trees. There is a strong interest to actively manage old growth stands in the Northern Rocky Mountains to restore them to pre-settlement conditions and to protect them from harvesting, severe wildfire and stress-induced mortality. However, little is known on the responses of old growth trees to alternative management practices. We examined the effectiveness of several restoration treatments to improve the function of old growth ponderosa pine and western larch in western Montana and report results from five consecutive years after treatment implementation. The restoration treatments applied were: 1) Control: the old growth stand continued to be fire excluded (C), 2) Understory cutting followed by pile burning (pile burn = PB), 3) Understory cutting followed by broadcast burning (broadcast burn = BB), 4) Overstory thinning with understory cutting followed by pile burning (overstory thin and pile burn = OPB) and 5) Overstory thinning with understory cutting followed by broadcast burning (overstory thin and broadcast burn= OBB). In particular, we determined whether available soil moisture, whole-tree water use, foliage nitrogen content, branch-level foliage production and radial growth of old growth ponderosa pine and western larch changed in response to different restoration treatments. Results showed that treatment-induced changes in leaf nitrogen content and branch-level leaf production were generally largest the second season after treatment implementation and diminished over time. In contrast to leaf- and branch-level responses, whole-tree responses (water use and radial wood growth) persisted over time. These results combined with a tendency for reduced treatment differences in soil moisture over time, suggest that old growth ponderosa pine and western larch responded to restoration treatments with changes in biomass allocation. That is, in the short-term resources released due to the removal of the competing understory were apparently diverted to the existing amount of branches (hence the initial increase in branch-level foliage production), while in the long-term resources may have been diverted to the production new branches with their corresponding new foliage. Increase in above-ground growth may be responsible for the decreased treatment-induced differences in soil moisture observed over time (particularly during the fourth and fifth

season post-treatment). Overall, differences between specific restoration treatments were relatively small suggesting that amelioration of old growth tree function and growth is primarily accomplished by the removal of the vigorous Douglas-fir understory without necessarily involving prescribed fire. Results also suggest that additional thinning of the overstory may have small additional positive effects on western larch tree function.

Introduction

Prior to 1900 most larch (*Larix occidentalis*) and ponderosa pine-dominated stands (*Pinus ponderosa*) experienced frequent surface fires (Arno 1988, Martin 1982). These frequent low-intensity fires helped maintain open, park-like ponderosa pine and larch stands, where old growth trees (> 200 years old) were common. In the interior northwest, preferential harvesting of old growth trees combined with fire exclusion since the early 1900's has resulted in a successional replacement of open ponderosa pine and larch stands to stands of interior Douglas-fir (*P. menziesii* var *glauca*) on several million hectares (Keane et al. 1989; 1996). In addition to the loss of the highly valued old growth trees, ecological implications of this successional replacement include increased stand-level transpiration, increased interception of water and snow, decreased snow pack accumulation and an increase in evaporation of intercepted water. As a result of these changes, water loss to the atmosphere may increase and overall soil water availability decrease. Changes in biomass allocation may follow, resulting in a decrease of the above ground biomass production, and timber quality. Furthermore, increased density, canopy cover and LAI in fire excluded stands result in an increase of pathogen host availability. This combined with increased susceptibility to pathogen infection due to decreased resource availability (water and nitrogen), may result in a decrease of forest health (Kolb et al. 1998). In spite of these potential ecological implications relatively few studies have quantified changes in ecosystem properties such as nutrient cycling, water cycles and productivity resulting from fire suppression in the interior northwest (but see MacKenzie et al. *in press*).

Because of the combination of fire suppression and harvesting, old growth stands in the interior northwest are very rare. The inherent aesthetic and natural value of old growth trees has triggered a strong interest to protect the few remnant old growth stands from harvesting, severe wildfire and stress-induced mortality and to restore them to pre-settlement conditions. Studies on the responses of pre-settlement old growth ponderosa pine responses to restoration treatments have been conducted in the Gus Pearson Natural Area in Arizona (Feeney et al. 1998; Stone et al. 1999; Wallin et al. *in press*). However, data on old growth ponderosa pine and western larch physiological responses and ecological impacts (water and nutrient cycles and forest productivity) of different restoration practices in the interior northwest are completely lacking.

These data are crucial to ensure the effectiveness of potential restorations treatments and the maintenance of healthy old growth forests.

Objectives

The overall goal of this project is to assess the effectiveness of several management treatments to restore old growth ponderosa pine and western larch stands. The restoration treatments considered are:

1) Control: untreated fire-excluded old growth stand with a vigorous Douglas-fir understory
2) Understory cutting (removal of Douglas-fir) followed by pile burning (pile burn)
3) Understory cutting followed by broadcast burning (broadcast burn)
4) Overstory thinning with understory cutting followed by pile burning (overstory thin and pile burn)
5) Overstory thinning with understory cutting followed by broadcast burning (overstory thin and broadcast burn).

These treatments are intended to simulate different fire regimes ranging from no fire (control) to low intensity understory fire without (treatment 3) or with some overstory mortality (treatment 5). They also allow to separate the effects of fire (treatments 2 and 4) from the effects of decreased understory and overstory competition for resources on forest function (treatments 2 and 4).

Specifically, the questions addressed are:

1) Does understory removal release old growth ponderosa pine and western larch from competition for resources?

2) Does understory removal combined with overstory thinning of old growth trees release ponderosa pine and western larch to a greater extent than understory removal alone?

3) Does the response of old growth ponderosa pine and western larch change depending on the specific restoration treatment by which understory is removed (cutting + pile burning or cutting + broadcast burning)?

In particular, during the 2003 growing season we examined whether available soil moisture, whole-tree water use, foliage nitrogen content, foliage production, and radial wood increment of old growth ponderosa pine and western larch changed in response to the different restoration treatments applied in 1998 (6 years before). These treatments provide an extraordinary opportunity to *experimentally* assess changes in ecosystem properties due to fire suppression. Overall we hypothesized that decreases in stand density and canopy cover as a result of active management ameliorates the function and growth of old growth trees due to a release from competition for limited resources relative to control, fire-excluded stands. Therefore, remnant fire-excluded old growth forests may be at risk due to the stresses associated with the lack of frequent fires. Based on previous results at the same experimental site (Sala and Callaway 2003) and of results from post-settlement trees at other sites (Sala et al. submitted) we did not expect significant differences of old growth tree performance and soil moisture among the actively managed stands.

Experimental Approach

The Fire Sciences Laboratory (U.S. Forest Service, Missoula Montana) located an old growth remnant stand of ponderosa pine and western larch at the Grant Creek valley of the Lolo National Forest (Missoula, Montana). The stand had not burned in about 80 years and had never had tree harvesting. Because of the lack of disturbance by fire the understory was dominated by Douglas-fir. Most of the overstory ponderosa pine and western larch are 320 to 380 years old. The stand is located on a steep slope oriented South-West and is divided by a Forest Service road that runs perpendicular to the slope. The overstory of the upper portion of the stand (above the road) is dominated by western larch, while the lower portion (below the road) is co-dominated by ponderosa pine and western larch.

During the summer of 1998 the stand was subdivided into 5 plots. From down slope to up slope, the assigned treatments described above were: control, pile burn, broadcast burn,

overstory thin + pile burn and oversoty thin + broadcast burn. The two overstory plots are located above the road. All plots span the entire width of the old growth stand. Because of logistical restrictions, broadcast burning was assigned to the plots next to the road. The removal of the understory in treatment plots was performed in September 1998, while the burning (pile and broadcast burning) took place in March 1999.

Methods

Stand Function

Conifers respond to environmental change and stand structure both by leaf-level physiological changes and by reallocating biomass among photosynthetic and respiratory tissues (Kaufmann 1979; Graham and Running 1984; Whitehead et al. 1984; Callaway et al. 1994a,b; See also Gower et al. 1995 and Pallardy et al. 1995; Kolb et al. 1998; Nagel and O'Hara 2002; Lathan and Tappeiner 2002; McDowell et al. 2003). Here we document species-specific changes in foliage production, nitrogen content and whole-tree water use in response to treatment implementation 5 seasons after treatments were applied.

Leaf production and Physiology

Branches of ponderosa pine and western larch (8-14 trees per treatment, one branch per tree) were sampled in late August 03 from all plots to determine foliage biomass. For ponderosa pine, needles of the three most recent foliage cohorts were detached, kept in separate bags and dried for 72 h at 65 C. For western larch, foliage biomass was determined for 30 cm-long terminal branch sections. The youngest fully mature leaf tissue for each ponderosa pine and western larch sampled were sent for analyses of total leaf nitrogen content and stable carbon isotope ratios. Stable carbon isotope data were used as long-term indicators of the ratio between leaf internal to ambient CO_2 concentrations (C_i/C_a) which is often correlated with water use efficiency (WUE, e.g. Marshall and Zhang 1994). Analyses were conducted at the Stable Isotope Laboratory of the University of California, Davis. Carbon isotope ratios were referenced to the Pee Dee Belemnite standard.

Whole-tree water use

Sap flow was measured using the heat pulse method, which uses pulses of heat as markers in the sap stream. Sap flow rates for ponderosa pine are generally very low and often fall below the sensitivity level of the heat pulse method used here (Sala and Callaway 2000, 2001, 2002). Therefore, treatment effects on whole tree water use are difficult to detect. In contrast, western larch, a deciduous conifer with larger xylem vessel diameters, exhibits much higher sap flow rates. Consequently, during the 2003 summer we emphasized on water use in western larch as an indicator species of potential treatment effects on water availability and tree water use. A similar approach was taken during the 2000 and 2001 summers. In addition, during the 2003 summer we tried a new method to measure sap flow in ponderosa pine designed to increase sensitivity at very low sap flow velocities (see below).

Sap flow in western larch was monitored semi-continuously from the end of June to mid-September 2003. Five to eight trees were measured per treatment in the control, pile burn and broadcast burn treatments and three-four trees in the overstory thin + pile burn and overstory thin + broadcast burn treatments. Sap flow for pines in the control, pile burn and broadcast burn treatments was measured during the last week of July and again the second week in August. During these periods sap flow measurements for larch trees on these same treatments were interrupted due to lack of sufficient equipment to measure all trees at once. Three to eight pines were measured simultaneously per treatment.

Sap flow probes (Thermalogic, Pullman, Washington) used for western larch and ponderosa pine in August and a subset of ponderosa pines in July consisted of two 1.25-mm needles inserted in the sapwood: a lower heater needle and an upper thermocouple needle installed 6 mm above the heater. Each thermocouple needle had three individual thermocouples regularly spaced along the length of the needle (so that the heat pulse was sensed at increasing sapwood depths). Probe lengths varied from 30 mm (inserted in the smallest trees) to 35 mm (inserted in the larger trees). Data loggers (Models CR10 and 21X, Campbell Scientific, Logan, Utah) were used to control the relays operating the heaters and record the data. One probe was inserted per tree on the west-side of the trunk at a height of approximately 2 m. Once installed, probes were insulated with 6-cm thick foam and wrapped with padded reflective material to minimize the effect of external temperature fluctuations. The convective velocity of a heat pulse (V) was calculated as (Cohen et al. 1981; Schiller and Cohen 1995):

$$V = (r^2 - 4\,k\,t_m)^{1/2} / t_m \qquad \text{(equation 1)}$$

where r is the distance between the heater and the thermocouple needles (6 mm), k the thermal diffusivity of wet wood, and t_m the time to the maximum temperature rise following the heat pulse. When no sap flow takes place, V = 0 and equation 1 yields:

$$k = r^2 / 4t_{m0} \qquad \text{(equation 2)}$$

where t_{m0} is the time to maximum temperature rise at zero flow. Combining equations 1 and 2 yields:

$$V = r\,(1-t_m/t_{m0})^{1/2} / t_m \qquad \text{(equation 3)}$$

Sap flux density at each sapwood depth (J_i) is calculated as:

$$J_i = V\,\rho c / \rho_w c_w \qquad \text{(equation 4)}$$

Where ρc and $\rho_w c_w$ are the volumetric specific heat of wood and water, respectively.

Zero sap flow conditions were assumed to occur at dawn (4 A.M., local time). The volumetric specific heat (Campbell et al. 1991) of wet wood was determined gravimetrically from sapwood samples taken in 6 trees of each species. For the purposes of this report our emphasis will be on relative differences in sap flow velocity between the different treatments during each measurement period, rather than on absolute values.

On a subset of pines in July 2003 (3 from each treatment) we tried the heat ratio method (HRM) designed to increase sensitivity at very low sap flow velocities (Burgess et al. 2000). The method consists in inserting a three 1.25 mm diameter, 35 mm long needle probe in the sapwood. The middle needle is a heater, and the lower and upper needles are thermocouple needles installed 6 mm above and below the heater. As for the heat pulse method, each thermocouple needle had three individual thermocouples regularly spaced along the length of the needle. An eight second pulse was sent to the heater every 30 minutes. The Heat Ratio Method estimates sap flow velocity from the ratio of heat sensed in the upper and lower thermocouple needles. Such ratio accounts for non-water driven heat dissipation (i.e. via wood only), which can be high at very low sap flow velocities and can obscure sap flow measurements when using the regular heat pulse method. The heat ratio method, therefore, is very sensitive at low sap flow velocities. Unfortunately, however, and contrary to our expectations, we were unable to adapt our current heating system to the new probes and we were unable to use the new method as intended. Therefore data reported is based on a subset of pines per treatment which were equipped with heat pulse probes as in previous years.

Weather variables (relative humidity, air temperature, global radiation and wind velocity) were measured concurrently with sap flow measurements at 60 second intervals and averaged every 30 min. in a nearby clearing. Potential evapotranspiration (PET) was calculated from these measurements using the Penman-Monteith equation as modified by van Bavel (1966), which gives an estimate equivalent to open water evaporation under a given set of environmental conditions.

Soil moisture

Seasonal changes in soil moisture were monitored in each treatment with a Frequency-Domain Reflectometer. In each plot 15 to 2 inch diameter PVC pipe were inserted in the soil as deep as substrate conditions permit. Eight additional pipes were located outside each treatment plot to quantify the influence of the slope gradient (or microsite) on soil moisture. Soil moisture was measured periodically at 15, 30 and 40 cm deep during the growing season by inserting the probe in the pipe at the desired depth.

Data analyses

Treatment differences in soil moisture at each soil depth were analyzed using one way ANOVA per date. Similar separate analyses were performed for measurements outside each plot, which measure the effect of the slope gradient or microsite (the measures in the treatment plots indicate the combined effect of treatment and microsite). Treatment differences of tree water use were assessed from maximum sap flow velocity values measured in the outer sapwood. Maximum values occurred from 1400 to 1800 in June and July, from 1300 to1700 in August and from 1200 to 1600 in September). Water transport is typically higher in the outer, most recent sapwood and decreases in the inner sapwood. Therefore, maximum sap flow velocity in the outer sapwood was used as an indicator of maximum tree water transport. For simplicity, for western larch and Douglas-fir, where measurements were semi-continuous, only selected days during the summer were analyzed for treatment differences. Per each species, treatment differences in maximum sap flow velocity were analyzed using one way ANOVA per selected date. Treatment differences in foliage production, bud length (for ponderosa pine), nitrogen content, carbon stable isotope ratios, cone production and radial wood increment were also analyzed with a one-way ANOVA. For ponderosa pine analyses were done separately for

each leaf cohort. Differences between specific treatments were tested using the Least Significant Difference test. Data were log transformed when necessary to meet ANOVA assumptions of normality.

Results and Discussion

Summary of previous results (pre-treatment to four seasons post-treatment)

Old growth ponderosa pine and western larch showed remarkable rapid responses to the variety of restoration treatments applied in this study. Overall, pre-treatment measurements (1998) indicated no significant differences in soil moisture and physiological indicators of trees assigned to the different treatments (Appendix 1). On the contrary, pre-treatment measurements showed a tendency for higher physiological activity and foliage production in control trees located at the base of the slope. In contrast, during the first season after treatment implementation (1999), significant treatment-induced increases in soil moisture and a tendency for treatment-induced amelioration of foliar production and whole-tree water use were already apparent (Appendix 1; Sala and Callaway 2000). The greatest treatment-induced responses for the parameters measured were observed two seasons after treatment implementation (2000; Appendix 2; Sala and Callaway 2001). Increased performance for western larch in treated plots during the 2000 season was evident from; 1) significantly higher sap flow during the driest part of the summer relative to control plots, 2) increase in foliar nitrogen content in trees from all treated plots relative to the control plots and 3) slightly higher foliage production (although not statistically significant) in trees from all treated plots relative to the control plot. Increased ponderosa pine performance was manifested in: 1) higher sap flow in the treated plots relative to the control plot, 2) highly significant increases in foliage production and bud size in trees from the treated plots and 3) significantly higher leaf nitrogen content in the broadcast burn plot relative to the control and thin plots. Most of these treatment-induced responses persisted through the third season after treatment implementation (2001; Appendix 3; Sala and Callaway 2002), although responses were not as apparent as in 2000. Increased performance for western larch in treated plots during the 2001 season was evident from: 1) significantly higher water use during the driest part of the summer relative to control plots, 2) tendency for higher foliage production in trees from all treated plots relative to the control plot, and 3) tendency for higher radial wood increment in trees from all treated plots relative to the control plot. No differences in foliar nitrogen content

were observed for western larch in the different treatments during the 2001 season. For ponderosa pine, increased performance during the 2001 season was reflected in: 1) higher sap flow in the treated plots relative to the control plot during July; 2) increases in foliage production and bud size in trees from treated plots; 3) higher leaf nitrogen content in the broadcast burn plot relative to the control and thin plots; and 4) tendency for higher radial wood increment in trees from treated plots. During the fourth season after treatment implementation (2002) restoration treatments continued to have some positive effects on soil moisture and tree performance. However, differences during the 2002 growing season were generally smaller than those observed in previous years and only apparent for some of the response variables measured (Appendix 4; Sala and Callaway 2003). Overall, soil moisture during the 2002 season tended to be greater in control plots than in the rest of the treatment plots, particularly at 40 cm depth and later in the summer when soil moisture was lower. Lower soil moisture in control plots was consistent with generally higher water use efficiency in both ponderosa pine and western larch. Consistent with these differences, radial wood increment after the 2002 season in ponderosa pine and western larch was generally higher in the restoration treatment plots relative to the control. For western larch we also found significantly higher leaf nitrogen in the restoration treatments. In contrast to results from previous years, leaf biomass produced during 2002 for both ponderosa pine and western larch did not differ among treatments.

These results clearly demonstrate a positive effect of the different restoration treatments applied on the physiological performance and growth of old growth trees. Overall, however, differences between specific restoration treatments were small suggesting that amelioration of old growth tree function and growth in the short-term (1-5 years) may be accomplished via the removal of the Douglas-fir understory that develops in the absence of fire without necessarily involving fire (but see below).

2003 Results (five seasons post-treatment)

Results after five growing seasons from the implementation of restoration treatments continue to show an overall significant positive treatment effect on the performance of old growth ponderosa pine and western larch. Old growth trees in plots where the Douglas-fir understory was removed (independent of the specific treatment by which it was removed) generally showed increased wood radial growth rates and higher water use during the peak of the

summer (late July and early August). However, consistent with results during the third and fourth season after treatment implementation (see Appendixes 3 and 4), treatment effects on the response variables measured were less apparent and not significant for all response variables analyzed (see below).

Soil moisture within and outside each treatment plot was highest at 40 cm and lowest at 15 cm (Figures 1-3). For all treatments and soil depths, soil moisture was highest early in the growing season and decreased gradually to minimum values later in the season. Differences in soil moisture among treatments were very small and only apparent at 40 cm depth (Figures 1-3), suggesting highest fine root density at this depth. Soil moisture at 40 cm throughout the summer in the 'outside' (but adjacent to) treatment plots tended to be lower next to the control plot than next to the rest of the treated plots, suggesting a microsite effect independent of the treatment effect (Figure 1). While higher soil moisture down the slope is counterintuitive, these results are consistent with those obtained during the previous growing seasons (Appendixes 1-4). Differences in soil texture and micro-topography may explain higher soil relative water content in the control plot. During July and August 2003, differences in soil moisture (at 40 cm) between the control and active treatment plots were higher within the treatment plots than outside the treatment plots (Figure 1), suggesting a small net treatment effect. Within the treatment plots there were statistically significant differences between the control and the broadcast burn, overstory pile burn and overstory broadcast burn plots. However, there were no statistically significant differences in the outside plots. As during the 2002 season (Appendix 4), soil moisture at 40 cm tended to be higher in the overstory thin + pile burn plot throughout the season. At the end of the season (late August and September) both overstory thin + pile burn and overstory thin + broadcast burn treatments tended to have higher soil moisture, although statistically significant differences were mostly with respect to the control plot only. The tendency for higher soil moisture at 40 cm in the overstory thin + pile burn and overstory thin + broadcast burn treatments is consistent with results during the 2000 and 2001 growing seasons (Appendixes 2 and 3) when within the treatment plots (but not outside) soil moisture tended to be also higher in the OPB and OBB treatments. These results suggest that the decrease in tree density in the plots where the overstory was thinned (OPB and OBB) resulted in larger increases of soil water availability relative to the PB and BB treatments. With the exception of higher soil moisture in the overstory thin + pile burn treatment early in the season, soil moisture differences

between the different active treatments were generally not significant. These results suggest that the specific treatment the understory was subjected to once it had been removed (pile burning vs. broadcast burning) had little effect on soil water availability. Treatment effects on soil moisture (% volume) at 30 and 15 cm were non-detectable during the 2003 season (Figures 2 and 3). Treatment effects on soil moisture were highly significant the first and second season after treatment implementation (Appendixes 1 and 2) but decreased over time (see Appendixes 3-4). This may be due to a combination of factors including year-to-year variations in climate and the fact that treatment-induced increases in tree water use and growth (Appendixes 1-4) may partially offset the effects of the understory removal on soil water resources.

As in previous seasons (Appendixes 1-4), maximum sap flow velocity during the summer of 2003 was much higher for larches than for pines (Figures 4 and 5). This is expected as western larch is a deciduous species that maximizes resource capture during the growing season. For simplicity, only maximum sap flow velocity during selected clear days at periodical intervals is shown for western larch. Maximum sap flow velocity was highest in July and declined strongly as the summer advanced (Figure 4). During June and early July (days 180 and 187) there were no statistically significant treatment differences in maximum sap flow velocity. However, on days 193 and 221 (July and early August), sap flow velocity in trees in the control plot declined to significantly lower values ($P < 0.01$) than for trees in the remaining treated plots (Figure 4). On days 248 and 268 (end of August and mid-September) there were no significant treatment differences. Therefore, treatment differences are highest at the peak of the summer coinciding with strong decreases of soil water availability (Figure 1) and disappear later in the summer when all treatments appear to be limited by soil water deficits. These results are similar to those from previous year when treatment effects are most apparent during the peak of the summer (Appendixes 1-4). Results are also consistent with less negative carbon isotope ratios in control ponderosa pine and western larch trees at the end of the 2002 season (Appendix 4; results for the 2003 season are not yet available) indicating increased water use efficiency and stomatal closure in control trees. Consistent with this, McDowell et al. (2003) reported decreased water use efficiency in ponderosa pine in response to reductions in stand-level basal area. Fenney et al. (1998) and Wallin et al. (*in press*) also reported less negative water potential (lower water stress) in ponderosa pine in response to restoration treatments. Throughout the season, maximum sap flow velocity tended to be higher in trees from the pile-burn treatment with significant

differences on day 221 (early August; Figure 4). We do not have an explanation for the observed higher sap flow velocity in the pile burn treatment as soil moisture (Figure 1) and foliage production (see below) in this treatment were no different from other treatments. Sap flow velocity for ponderosa pine was generally below the accuracy level of the method used. Therefore, the differences we report here need to be taken with caution and only as a qualitative measure of potential treatment effects. Average maximum sap flow velocity of ponderosa pine at the end of July was significantly higher in the treated plots but only when the pile burn and broadcast burn treatments were combined ($P < 0.05$; Figure 5). No treatment differences were detectable in August due to extremely low values and noisy data. As for western larch these results indicate that the removal of the understory increased the amount of water available for the old growth ponderosa pine trees. No differences in maximum sap flow were detected between the pile burn and the broadcast burn treatments suggesting that, once the competing understory was removed, the specific restoration treatment did not affect water availability to old growth trees.

Needle nitrogen content in ponderosa pine at the end of the 2003 season (five seasons after treatment) did not differ between treatments (Figure 6). For western larch needle N content in the broadcast burn and overstory thin + broadcast burn treatments did not differ from the control but values for the pile burn and overstory thin + pile burn treatments were significantly higher ($P < 0.05$) than in the control (Figure 6). Results from 1999 and 2002 (Appendixes 1 and 4) indicated that treatment differences for the understory shrub *Spirea* were only apparent the first growing season after treatment implementation (1999) when leaf N was higher in the broadcast burn and overstory thin+ broadcast burn treatments (Sala and Callaway 2000). These results suggested that temporary increases of soil available nitrogen due to prescribed fire (Covington and Sackett 1986, 1992; White 1996; DeLuca 2001) were primarily used by fast growing understory species. The lack of treatment-induced effects on leaf N in old growth ponderosa pine and western larch the first season after treatment implementation indicated that such initial flush of available soil N was not used by the old growth trees. However, at the end of the second season after treatment implementation (2000) leaf N content in western larch was significantly higher in all treatments relative to the control and for ponderosa pine values were also significantly higher in the broadcast burn treatment relative to the control (Appendix 2). These results suggested that reduction of competition for resources by removing the Douglas-fir

understory in the actively managed stands (by either thinning alone of thinning followed by burning) had a delayed positive effect of leaf N content of the old growth trees. In 2001 (3 seasons after treatment) we did not find significant treatment differences for western larch, while ponderosa pine from the broadcast burn treatment continued to shown higher leaf N content than in the control (Appendix 3). Results for the fourth growing season after treatment implementation (2002; Appendix 4), in contrast, showed no differences for ponderosa pine but higher leaf N content for western larch in most treatments relative to the control (the broadcast burn being the exception). Five years of needle N content data show a consistent pattern for ponderosa pine: no treatment effect the first season after treatment implementation (Appendix 1), increased leaf N content in the broadcast burn treatment the second and third season after treatment implementation (Appendixes 2 and 3) and no treatment effects the fourth (Appendix 4) and fifth season (Figure 6) after treatment implementation. Lack of treatment differences during the fourth and fifth season after treatment implementation may be due to a dilution effect. That is, increased available N in response to the removal of the competing understory is diverted to the production of new foliage rather than to an increase of needle N content. For western larch, only the two overstory thin treatments showed treatment effects after the first season of treatment implementation suggesting a positive combined effect of the overstory thinning and understroy removal (Appendix 1). By the second season after treatment implementation (Appendix 2) all restoration treatments resulted in increased leaf N content. Such treatment-induced effects were not apparent the third season after treatment implementation (Appendix 3) but showed up again the fourth season (with the exception of the broadcast burn treatment) when treatment effects were most apparent for the pile burn and overstory thin + pile burn treatments (Appendix 4). Interestingly, results for the fifth season after treatment implementation (2003; Figure 6) are consistent with those in 2002 with treatment effects most apparent in the pile burn and overstory thin + pile burn treatments and non significant for the broadcast burn and overstory thin + broadcast burn treatments. Western larch is a deciduous species which shows substantial retrieval of leaf N before leaf fall. Because we sampled foliage at the end of the summer, it is likely that the lack of treatment-induced differences in western larch in 2001 was due to an earlier retrieval of nutrients before leaf fall as a consequence of year to year differences in leaf phenology. Some general conclusions may be drawn from these results. Most notably, there were some important differences on how ponderosa pine and western larch responded to the

restoration treatments: ponderosa pine leaf N content increased to broadcast burning but not to pile burning. In contrast, western larch initially responded to all treatments but by the fourth and fifth season post-treatment responses were strongest for the pile burn treatments than for the broadcast burn treatments. Both, fire and thinning have been shown to cause substantial, short-term increases (up to one year) in inorganic nitrogen pools (Kovacic et al. 1986, White 1986, Covington and Sackett 1992, Monleon et al. 1997, DeLuca and Zouhar 2000) and transformation rates in the mineral soil of ponderosa pine systems (Kaye and Hart 1998 -but see Monleon et al. 1997). However, the forms of nitrogen directly or indirectly (via mycorrhiza) available in the soil may differ between broadcast burning and thinning due to different effects on soil microbial and fungal communities and on biochemistry resulting from the two type of disturbances. Branch-level foliage production (Figure 7) and growth (Figure 10) in ponderosa pine did not differ between the pile burn and broadcast burn treatments. Therefore, differences in needle N content in ponderosa pine in the pile burning and broadcast burning treatments do not appear to result from differences in growth and dilution effects. Rather, they may reflect a specific fire-induced response in ponderosa pine. Western larch in contrast, appeared to initially benefit from all treatments (most likely due to the removal of the competing understory). More detailed analyses on western larch biomass allocation, understory and nitrogen uptake dynamics are needed to understand why over time effects become stronger for the pile burn treatments.

Biomass of ponderosa pine needles of the four most recent leaf cohorts did not differ between control and treated plots (Figure 7). This is consistent with results observed the fourth season post-treatment (Appendix 4). Strong effects on branch-level foliage production were observed he second and third season post-treatment (Appendixes 2 and 3). Most likely, initial treatment-induced increases in needle biomass are followed by increased branching and overall leaf production (i.e. new foliage is allocated to new branches rather than to existing branches). Such interpretation is consistent with increased radial wood growth five seaons post-treatment (see below). As in previous years, total length (Figure 8) of buds on terminal ponderosa pine branches sampled at the end of the 2003 growing season was higher in the treated plots although differences where statistically significant only for the pile burn treatment ($P < 0,05$). These results suggest that active management continue to have a positive effect on the development of new shoots 5 seasons after treatment implementation. There were no differences in ponderosa pine bud size between the pile burn and broadcast burn treatments. For western larch, total

foliage biomass along 30 cm-long terminal branch sections was higher for trees in the overstory thin + broadcast burn and overstory thin + Pile burn treatments relative to the rest of the treatments (Figure 9; $P<0.05$). These results are consistent with those in 2001 (Appendix 3) but somewhat different from those obtained at the end of the 2002 season when only the overstory thin + broadcast burn treatment was significantly higher (Appendix 4) than the rest of the treatments. We caution, however, that our sampling protocol for western larch is approximate and subjected to substantial variation. Overall, however, foliage production results for western larch suggest a most pronounced effect in the treatments where the overstory trees where thinned. This is not surprising as increased light in these treatments relative to the understory removal only treatments may stimulate foliage production in this deciduous species.

The ratio of wood increment five years after treatment relative to five years before treatment was between 1 and 1.3 for ponderosa pine, western larch and Douglas-fir in the control plot indicating no substantial changes in wood radial growth rates after 1998, when treatments were implemented in the remaining of the plots (Figure 10). For ponderosa pine, values in the pile burn and broadcast burn plot were much higher than in the control plot ($P < 0.01$; Figure 10). There were no significant differences between the pile burn and broadcast burn treatments. For western larch wood radial growth were significantly higher in the pile burn, overstory thin+ pile burn and overstory thin + broadcast burn than in the control ($P < 0.05$; Figure 10). Values in the broadcast burn were also higher than in the control, but differences were not statistically significant. Radial wood increment for the overstory thin + broadcast burn were higher than in any other treatment ($P < 0.05$). There were no statistically significant differences between the pile burn, broadcast burn and overstory thin + pile burn treatments (Figure 10). These results indicate a substantial positive effect of active management on radial wood increment in old growth ponderosa pine and western larch. Feeney et al. (1998), Lathan and Tappeiner (2002) and McDowell et al. (2003) also reported significant basal area increments in ponderosa pine in response to understory thinning and basal area reductions. With the exception of the overstory thin + broadcast burn treatments, there were no differences between specific restoration treatments suggesting again that the most important treatment is the removal of the dense Douglas-fir understory. Higher values in the overstory thin + broadcast burn may indicate that the thinning of the old growth overstory has an additional positive effect on the remaining of the trees. This is consistent with higher branch-level foliage production in both the overstory thin

treatments (Figure 9). However, radial wood increment in the overstory thin + pile burn treatment was no higher than in treatments where only the understory was removed. No other response variable measured showed a differential response for the overstory thin+ broadcast burn treatment only, suggesting that higher radial wood increment in this particular treatment may reflect stochastic variation due to low sample size.

In summary, our results during the 2003 growing season (fifth growing season after treatment application) showed that restoration treatments resulted in higher sap flow velocities and generally higher radial wood growth. Consistent with results during the 2002 season (Appendix 4) there were no major differences in soil moisture and in leaf- and branch-level response variables. These results may indicate a change in biomass allocation in response to the restoration treatment from increased foliage in existing branches during the first initial years after treatment to new wood production (new branches and increased radial growth). While there was a strong positive effect of the understory removal, differences between specific restoration treatments were relatively small. However, additional thinning of the overstory may have some additional positive effect in western larch (there was no ponderosa pine in this treatment) Our results are generally consistent to those reported by Feeney et al. (1998) and Stone et al. (1999) for southwestern old growth ponderosa pine, who concluded that restoration thinning (of the understory) increased water uptake and nitrogen of pre-settlement trees (old growth) and that these changes contributed to greater rates of photosynthesis and stem radial growth. Both of these studies also reported small differences between thinning and thinning + burning treatments during the first season after treatment application. Results are also consistent with those of Covington et al. (2001) who, by using an ecological modeling approach, concluded that comprehensive restorative management is a viable long-term approach to conservation of key indigenous ecosystem characteristics. Latham and Tappeiner (2002) also reported long term positive effects of thinning treatments on the growth of old growth ponderosa pine in western Oregon. Interestingly these authors reported that most positive responses were found to occur between 5 and 25 years after treatment, while our results indicate immediate positive responses.

Conclusion

Data from five consecutive years after treatment application showed that restoration treatments designed to modify canopy structure towards that typical of pre-settlement times by

eliminating the dense Douglas-fir understory showed that leaf-level treatment-induced responses (e.g. leaf nitrogen and branch-level leaf production) were generally largest the second season after treatment implementation and diminished over time. In contrast to leaf- and branch-level responses, whole-tree responses (water use and radial wood growth) persisted over time. These results combined with a tendency for reduced treatment differences in soil moisture over time, suggest that old growth ponderosa pine and western larch responded to understory removal with changes in whole-tree biomass allocation. That is, in the short-term resources released due to the removal of the competing understory were apparently diverted to the existing amount of branches (hence the initial increase in branch-level foliage production), while in the long-term resources are diverted to the production new branches with their corresponding new foliage. Higher branch production in trees from treated plots may result in higher total amount of water used per tree, which may be responsible for the decreased treatment-induced differences in soil moisture observed over time (particularly during the fourth and fifth season post-treatment). Therefore, increased overall above ground biomass over time in trees from treated plots uses up excess soil water released by the removal of the Douglas-fir understory.

Overall, differences between specific restoration treatments were relatively small suggesting that amelioration of old growth tree function and growth is primarily accomplished by the removal of the vigorous Douglas-fir understory without necessarily involving prescribed fire. However, the ecological role of fire extends much beyond its effect on tree function, and long-term studies are necessary to assess the need to incorporate fire in restoration treatments. Results also suggest that additional thinning of the overstory may have small additional positive effects on western larch tree function.

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Figure Legends

Figure 1. Soil relative water content (% volume) at 40cm below the surface during 2003 (fifth growing season post-treatment) within the treatment plots (left) and outside each treatment plot (right). Treatments are: control (open triangles), understory removal followed by pile burn (P-Burn, open squares), understory removal followed by broadcast burn (B-Burn, open circles), overstory thin with understory removal followed by pile burning (O-PBurn, shaded squares) and overstory thin with understory removal followed by broadcast burning (O-BBurn, shaded circles). Bars are standard errors of the mean (N=15-20 per treatment and date for the treatment plots and 8 for the outside plots). Within a given date, significant differences between the control plot and the rest of treated plots are indicated with a star. The number on a given date denotes significant differences between the control plot and the indicated number of treated plots.

Figure 2. Soil relative water content (% volume) at 30 cm below the surface during 2003 (fifth growing season post-treatment) within the treatment plots (left) and outside each treatment plot (right). Treatments are: control (open triangles), understory removal followed by pile burn (P-Burn, open squares), understory removal followed by broadcast burn (B-Burn, open circles), overstory thin with understory removal followed by pile burning (O-PBurn, shaded squares) and overstory thin with understory removal followed by broadcast burning (O-BBurn, shaded circles). Bars are standard errors of the mean (N=15-20 per treatment and date for the treatment plots and 8 for the outside plots). Within a given date, significant differences between the control plot and the rest of treated plots are indicated with a star. The number on a given date denotes significant differences between the control plot and the indicated number of treated plots.

Figure 3. Soil relative water content (% volume) at 15cm below the surface during 2003 (fifth growing season post-treatment) within the treatment plots (left) and outside each treatment plot (right). Treatments are: control (open triangles), understory removal followed by pile burn (P-Burn, open squares), understory removal followed by broadcast burn (B-Burn, open circles), overstory thin with understory removal followed by pile burning (O-PBurn, shaded squares) and

overstory thin with understory removal followed by broadcast burning (O-BBurn, shaded circles). Bars are standard errors of the mean (N=15-20 per treatment and date for the treatment plots and 8 for the outside plots). Within a given date, significant differences between the control plot and the rest of treated plots are indicated with a star. The number on a given date denotes significant differences between the control plot and the indicated number of treated plots.

Figure 4. Maximum sap flow velocity for western larch in the different treatments (C=control: open triangles; PB= pile burn: open squares; BB= broadcast burn open circles, O-PB= overstory thin + understory pile burn: shaded squares; and O-BB= overstory thin + broadcast burn, shaded circles) during the 2003 growing season (date in Julian day). Bars are standard errors of the mean (N=3-8 per treatment). Stars indicate statistically significant differences between control and treated plots.

Figure 5. Maximum sap flow velocity for western larch (12 July 03) and ponderosa pine (27 July 03) five growing seasons post-treatment in the control plot (C) and the five restoration treatment plots: understory removal by pile burn (PB), understory removal by broadcast burn (BB), overstory thinning with understory removal by pile burn (O-PB) and overstory thinning with understory removal by broadcast burn (O-BB). Bars are standard errors of the mean (N=3-8). Within a given species, different letters denote statistically significant differences ($P < 0.05$). For ponderosa pine statistical differences were only observed when data for the two treated plots were combined.

Figure 6. Leaf nitrogen content of Ponderosa pine (white bars) and western larch (shaded bars) at the end of the 2003 growing season (five seasons after treatment) for the control (C), pile burn (PB), broadcast burn (BB), overstory thin+ pile burn (O-PB) and overstory thin + broadcast burn (O-BB) plots. Bars are standard errors of the mean (N=8-12). Within a species, different letters indicate statistically significant differences (LSD, $P < 0.05$).

Figure 7. Foliage biomass of four consecutive leaf cohorts of ponderosa pine in the control (black bars), understory removal followed by pile burn (P-Burn, gray bars) and by broadcast

burn (B-Burn, white bars) plots at the end of the 2003 growing season (five seasons post-treatment). Bars are standard errors of the mean (N=8-12). Within a given leaf cohort, different letters indicate statistically significant differences (LSD, $P < 0.05$).

Figure 8. Terminal bud length of ponderosa pine branches in the control, understory removal by pile burn (PB) and by broadcast burn (BB) plots at the end of the 2003 growing season (five seasons post-treatment). Bars are standard errors of the mean (N=6-10). Different letters indicate statistically significant differences (LSD, $P < 0.05$).

Figure 9. Foliage biomass in 30 cm terminal branch sections of western larch in the control (C), understory removal followed by pile burn (PB), by broadcast burn (BB), overstory thin + pile burn (OPB) and overstory thin and broadcast burn (OBB) plots at the end of the 2003 growing season (five seasons post-treatment). Bars are standard errors of the mean (N=8-10). Different letters indicate statistically significant differences (LSD, $P < 0.05$).

Figure 10. Radial wood increment ratio (width of the five tree rings after treatment/width of five rings before treatment) for Douglas-fir (black bar), ponderosa pine (white bars) and western larch (shaded bars) in control (C), pile burn (PB), broadcast burn (BB), overstory thin+ pile burn (O-PB) and overstory thin + broadcast burn (O-BB) plots at the end of the 2003 growing season. Bars are standard errors of the mean (N=6-11). Within a species, different letters indicate statistically significant differences (LSD, $P< 0.05$).

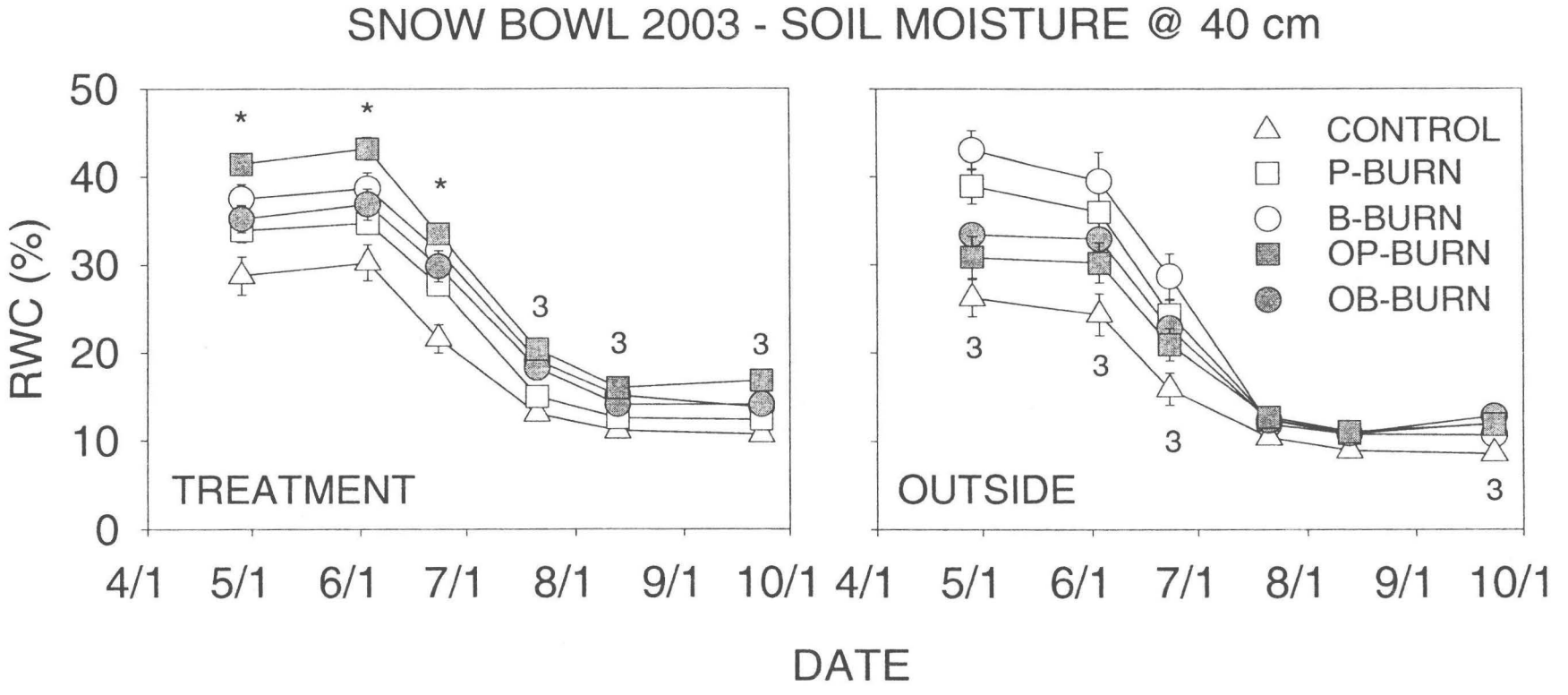
SNOW BOWL 2003 - SOIL MOISTURE @ 40 cm
RWC (%)
50
40
30
20
10
0
TREATMENT
OUTSIDE
CONTROL
P-BURN
B-BURN
OP-BURN
OB-BURN
*
*
*
3
3
3
3
3
3
3
4/1
5/1
6/1
7/1
8/1
9/1
10/1
4/1
5/1
6/1
7/1
8/1
9/1
10/1
DATE

FIGURE 1

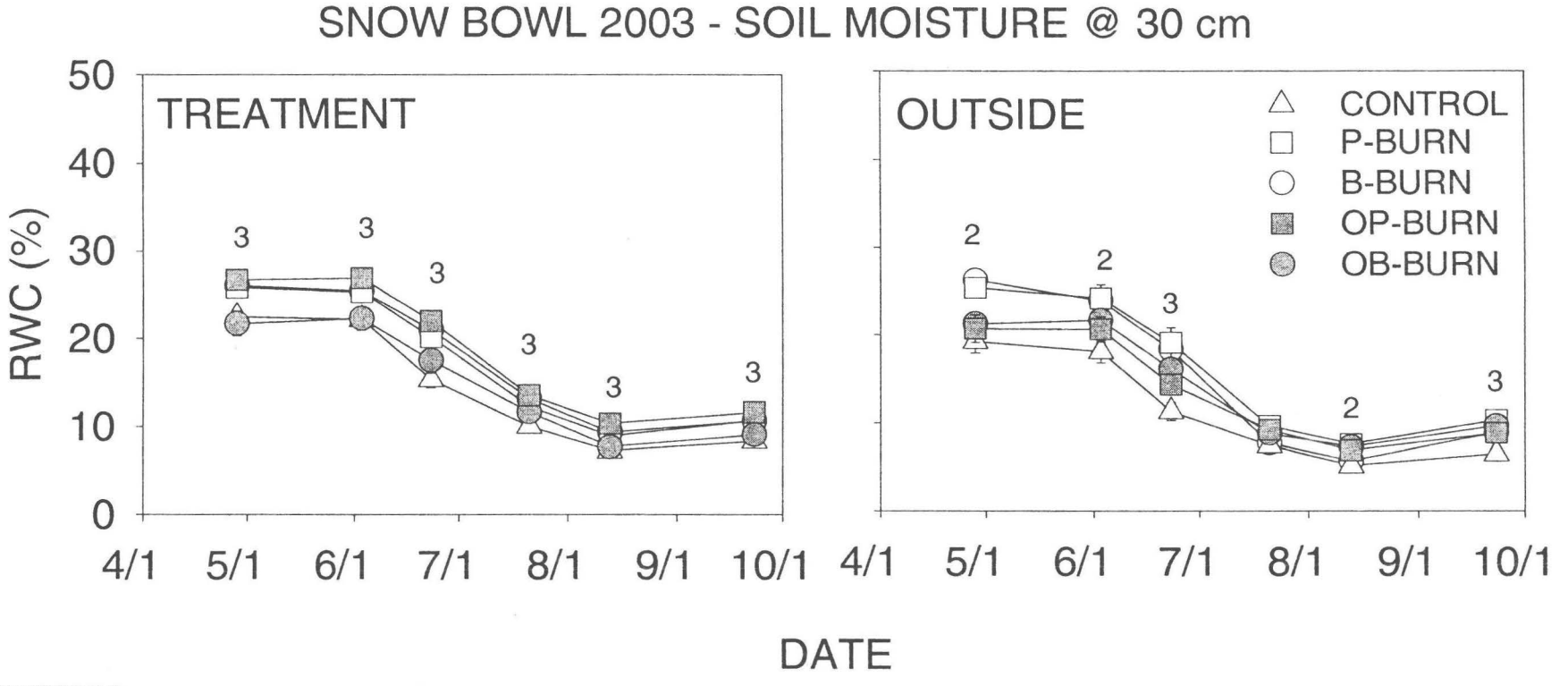
SNOW BOWL 2003 - SOIL MOISTURE @ 30 cm
TREATMENT
OUTSIDE
CONTROL
P-BURN
B-BURN
OP-BURN
OB-BURN
RWC (%)
50
40
30
20
10
0
3
3
3
3
3
3
2
2
3
2
3
4/1
5/1
6/1
7/1
8/1
9/1
10/1
DATE

FIGURE 2

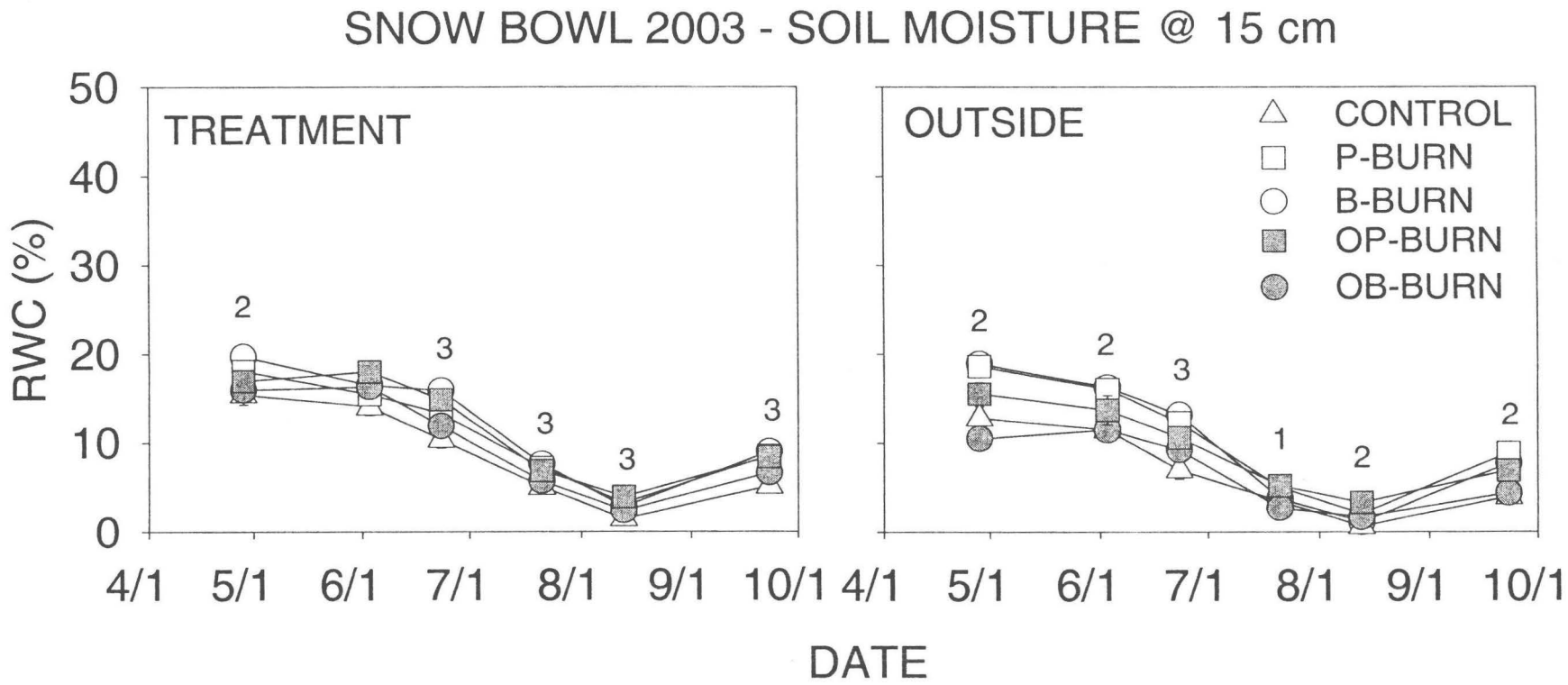
SNOW BOWL 2003 - SOIL MOISTURE @ 15 cm
TREATMENT
OUTSIDE
CONTROL
P-BURN
B-BURN
OP-BURN
OB-BURN
RWC (%)
50
40
30
20
10
0
2
3
3
3
3
2
2
3
1
2
2
4/1
5/1
6/1
7/1
8/1
9/1
10/1
DATE

FIGURE 3

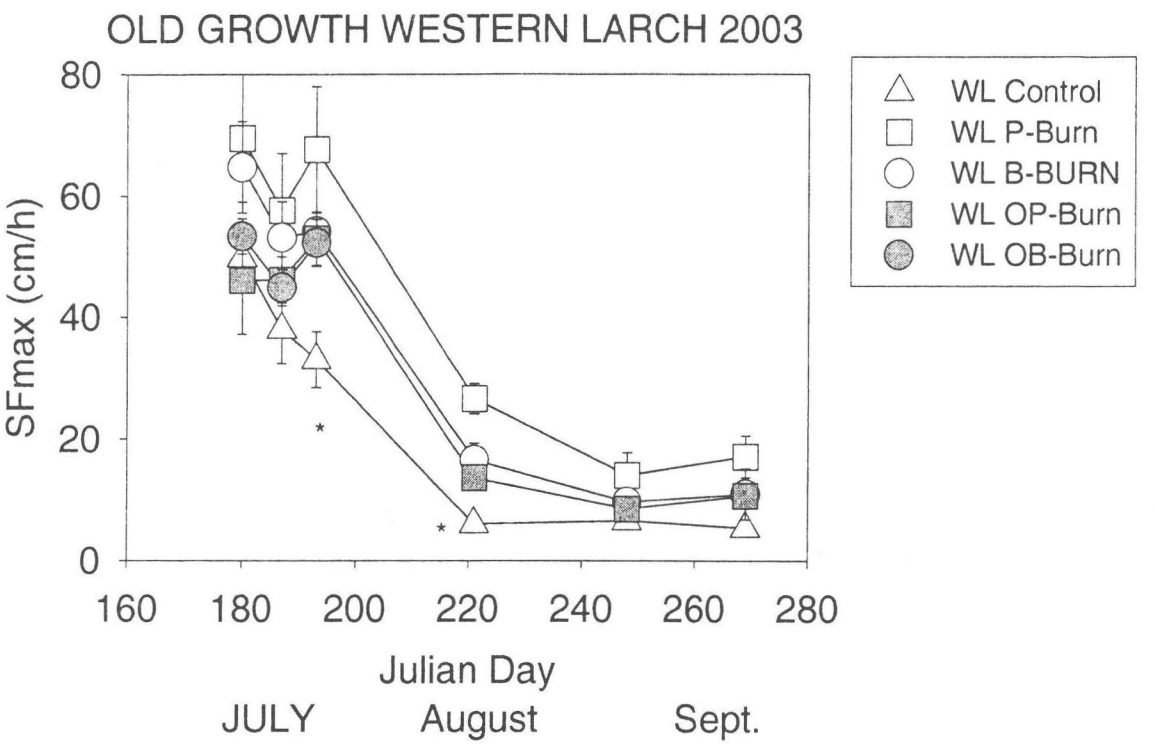
OLD GROWTH WESTERN LARCH 2003
SFmax (cm/h)
80
60
40
20
0
160
180
200
220
240
260
280
Julian Day
JULY
August
Sept.
WL Control
WL P-Burn
WL B-BURN
WL OP-Burn
WL OB-Burn

FIGURE 4

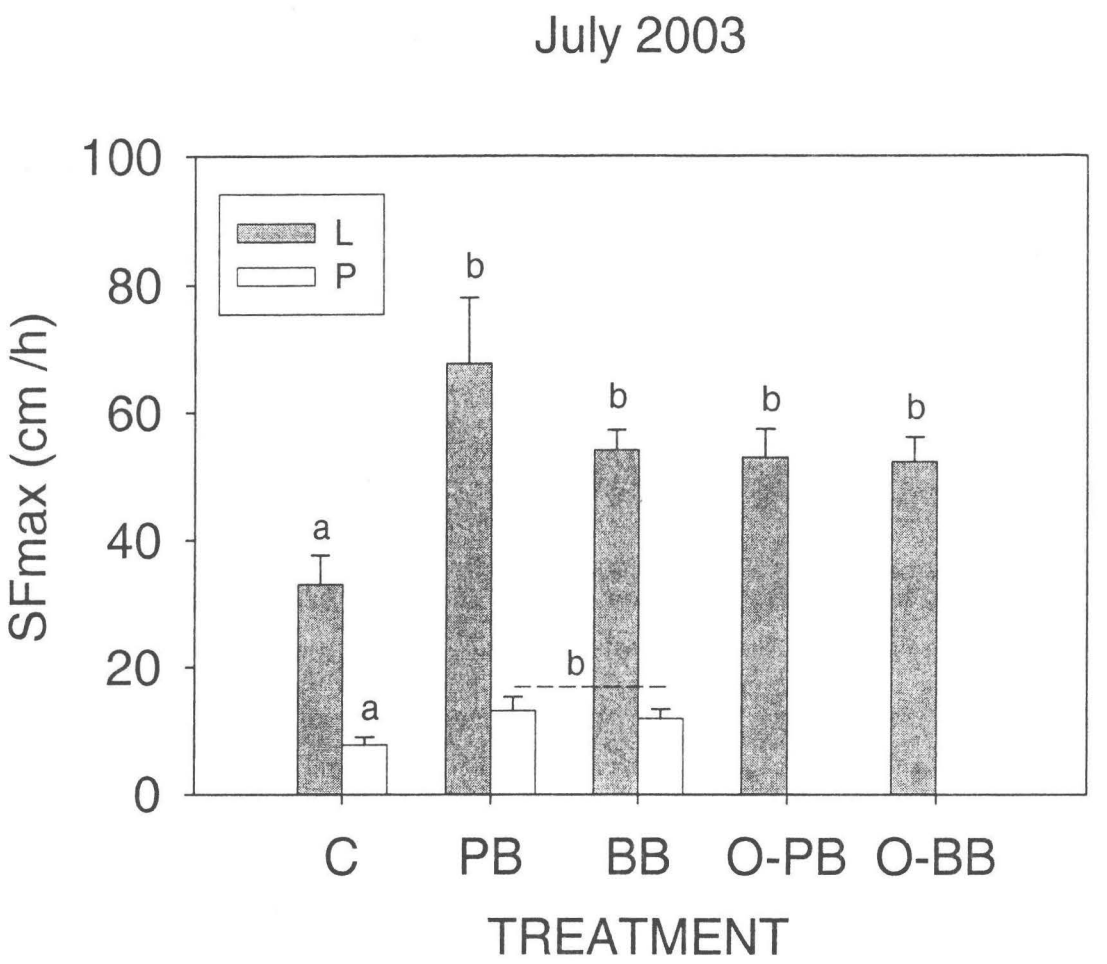
July 2003
100
80
60
40
20
0
SFmax (cm /h)
L
P
a
a
b
b
b
b
b
C
PB
BB
O-PB
O-BB
TREATMENT

FIGURE 5

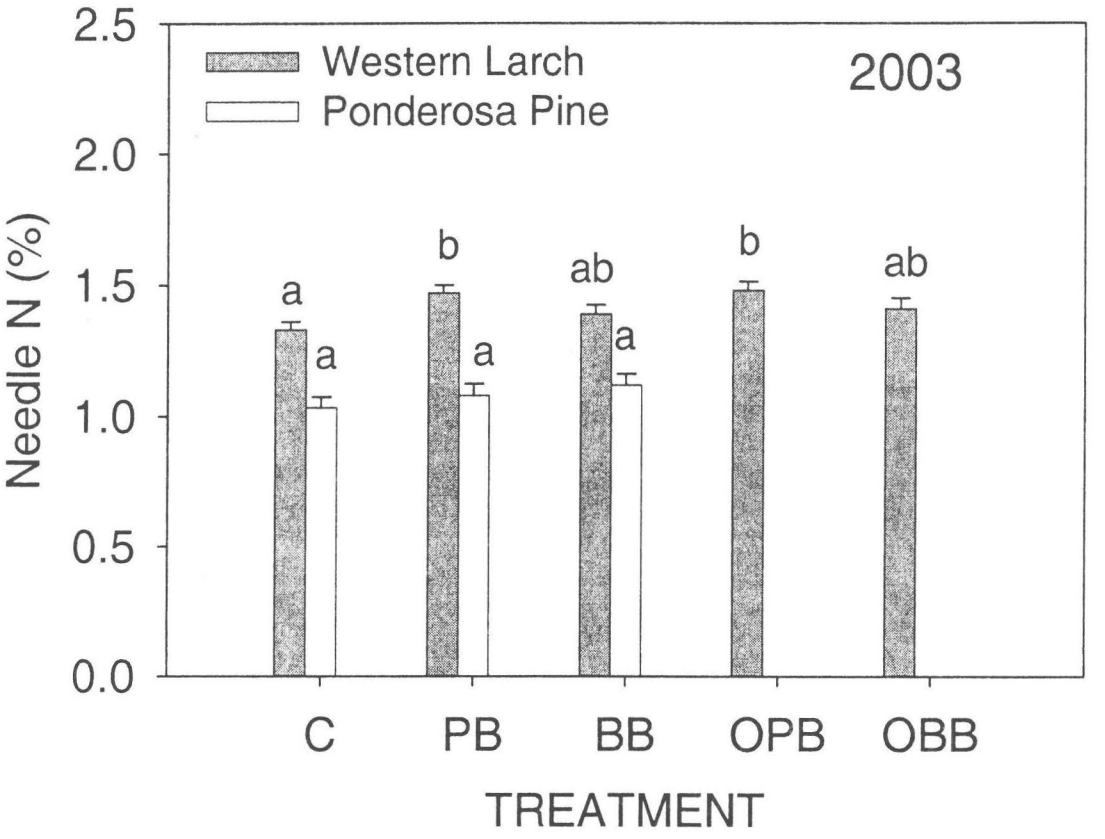
2.5
2.0
1.5
1.0
0.5
0.0
Needle N (%)
Western Larch
Ponderosa Pine
2003
a
a
b
a
ab
a
b
ab
C
PB
BB
OPB
OBB
TREATMENT

FIGURE 6

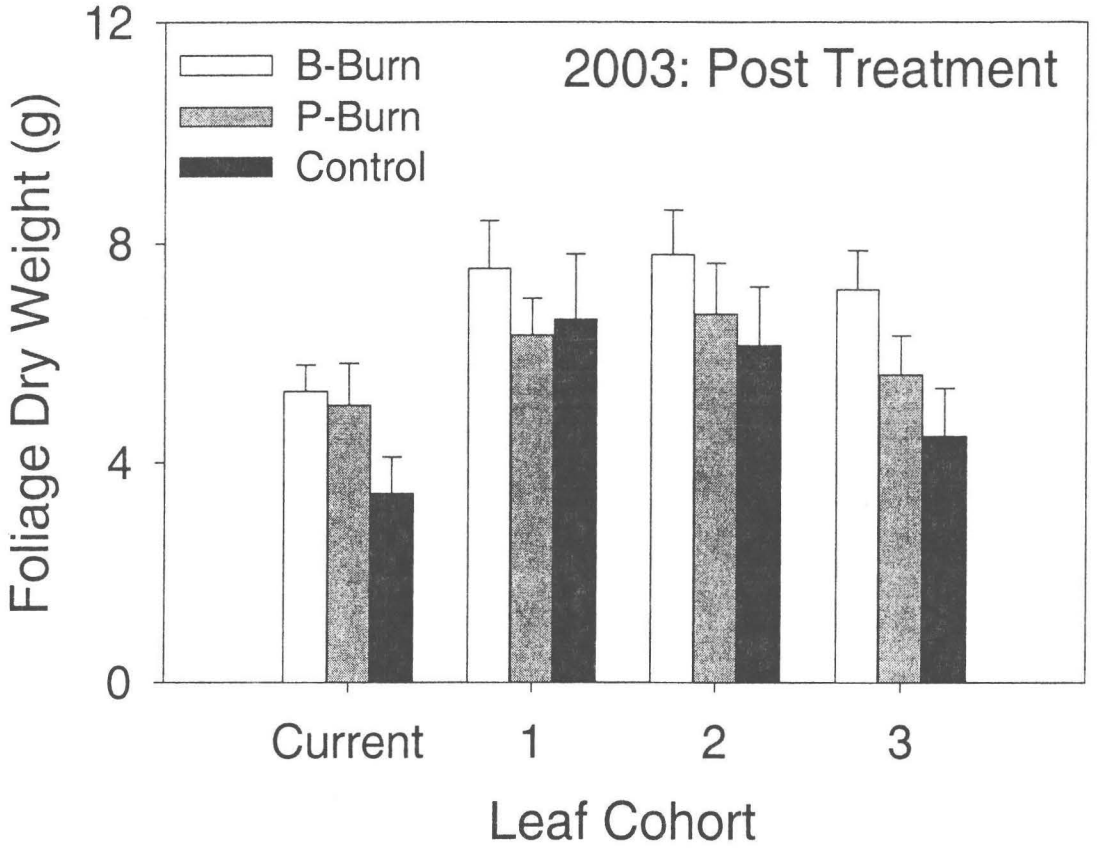
12
8
4
0
Foliage Dry Weight (g)
B-Burn
P-Burn
Control
2003: Post Treatment
Current
1
2
3
Leaf Cohort

FIGURE 7

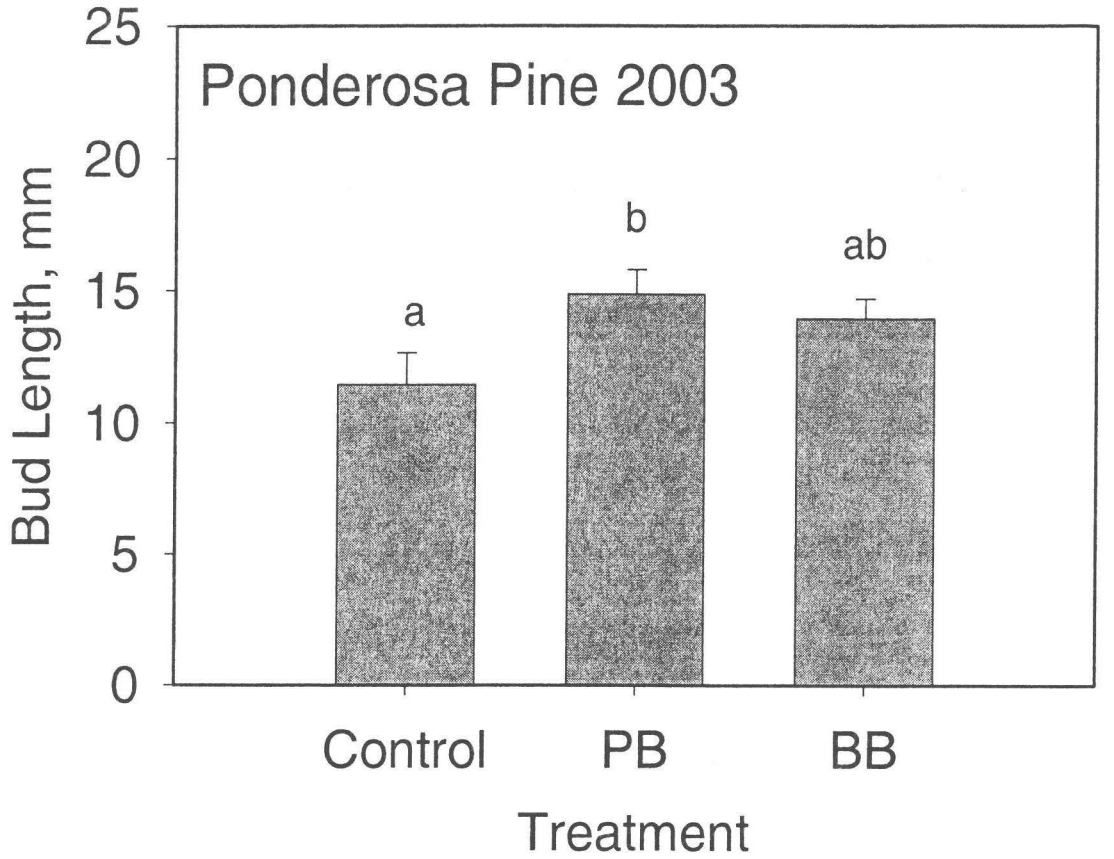
Ponderosa Pine 2003
Bud Length, mm
25
20
15
10
5
0
a
b
ab
Control
PB
BB
Treatment

FIGURE 8

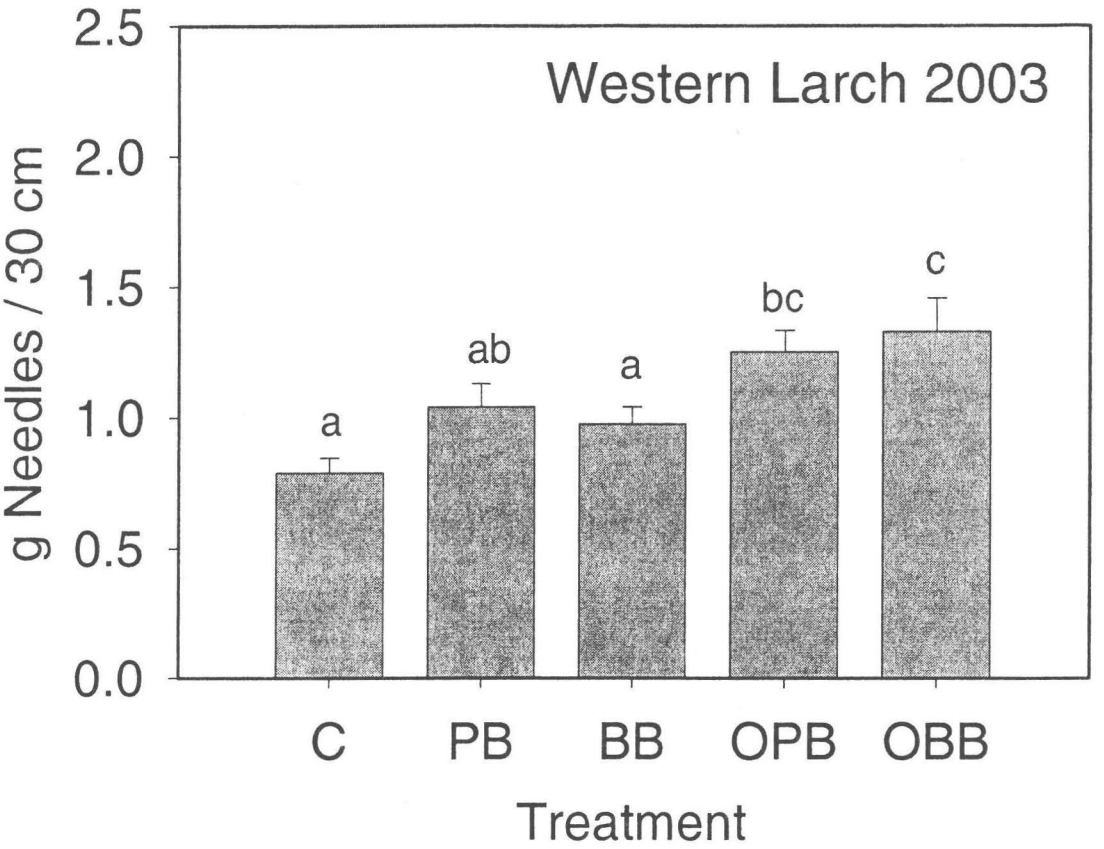
Western Larch 2003
g Needles / 30 cm
2.5
2.0
1.5
1.0
0.5
0.0
a
ab
a
bc
c
C
PB
BB
OPB
OBB
Treatment

FIGURE 9

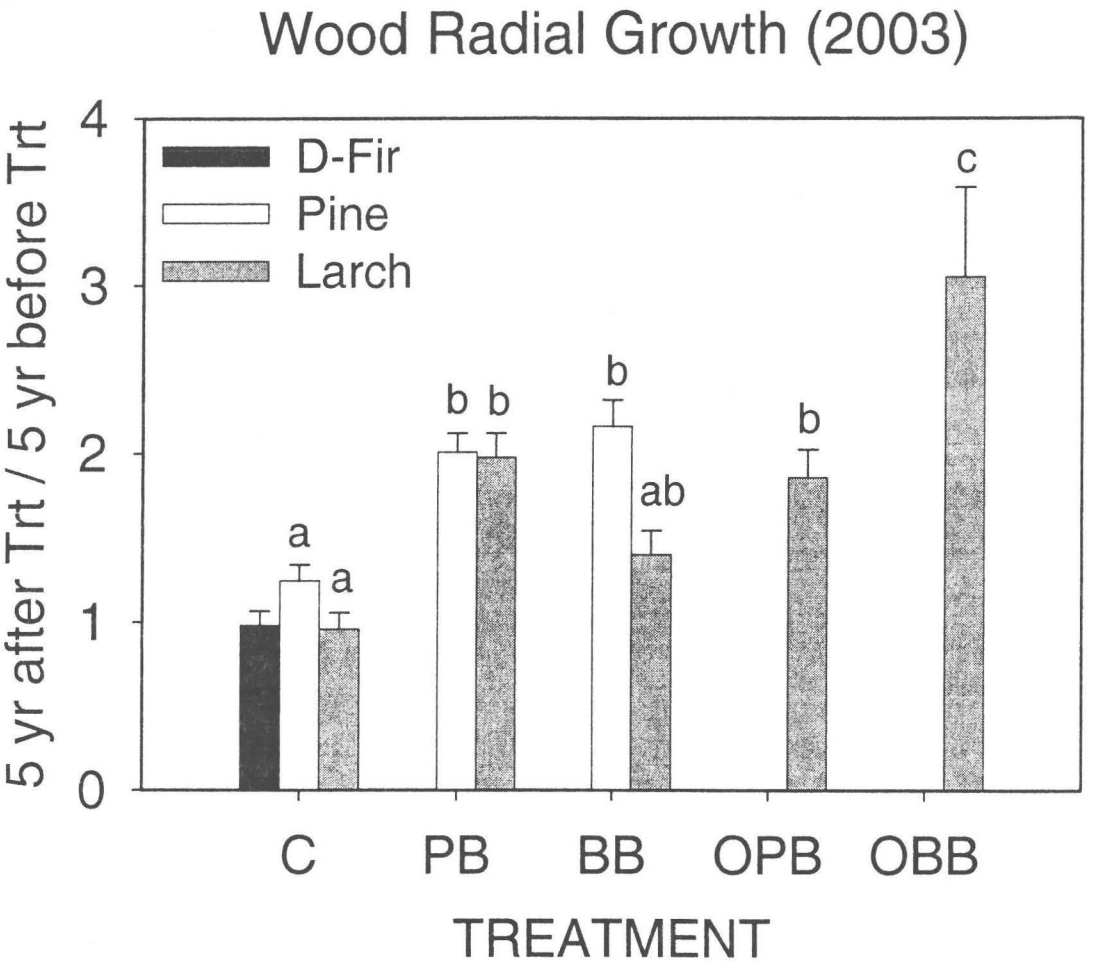
Wood Radial Growth (2003)
5 yr after Trt / 5 yr before Trt
4
3
2
1
0
D-Fir
Pine
Larch
a
a
b b
b
ab
b
c
C
PB
BB
OPB
OBB
TREATMENT

FIGURE 10